POSSIBLE FUNCTIONS OF HEAD AND BREAST MARKINGS IN CHARADRIINAE

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Cott (1966) proposed that many of the markings of shorebirds function as disruptive coloration. Tinbergen (1953) and many other authors suggest that many avian plumage patterns have signal function and reinforce display movements. Ficken and Wilmot (1968) and Ficken, Matthiae, and Horwich (1971) suggested that eye lines in many vertebrates may enhance their vision and enable predaceous species to locate and capture prey more effectively. The latter authors further suggest that the head markings of the Semipalmated Plover (*Charadrius semipalmatus*) probably serve mainly a disruptive coloration function, although they point out that a given pattern may serve several functions. Bock (1958) tentatively speculated that in Charadriinae the breast bands and head markings act as disruptive marks, especially for the nesting bird, and some of the markings also reinforce aggressive and courtship displays.

I have examined the literature concerning the Charadriinae in search of correlations that might provide suggestions on the relative importance of these possible functions in the subfamily as a whole, since many members of this group have complicated head and breast patterns and many have black lore lines. I have given special attention to (1) nest-site characteristics and (2) seasonal, sex, and age differences in coloration. I have also relied upon my 1969–72 observations on the Mountain Plover (*C. montanus*) in eastern Colorado for part of my conclusions.

Jehl (1968) lists 37 species in the subfamily Charadriinae in his system of shorebird taxonomy and I have followed his scheme.

RESULTS AND DISCUSSION

A variety of head and breast markings is found in Charadriinae with 24 basic patterns (Fig. 1) representing the 37 species in this subfamily. All species except the Hooded Dotterel (*C. rubricollis*) have an interrupted, i.e. non-uniform, head pattern (Table 1). Within the genus *Charadrius* there is a high incidence of a black lore line and a black crown patch and within the entire subfamily 21 species have distinct breast bands (Table 1). Breast bands when present usually consist of dark bands on light backgrounds, but in two cases light bands are against a dark background (Fig. 1).

Cott (op. cit.) states that the round shape of the eye is a conspicuous feature that needs to be concealed in many species and that eye lines commonly serve this function. Of the 37 species considered here, 27 have the

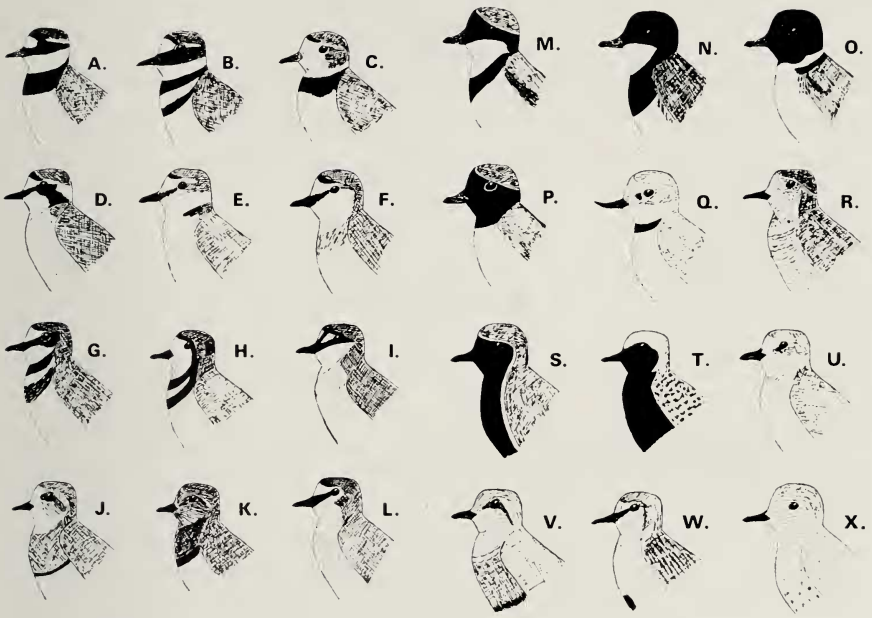

FIG. 1. Breeding adult head and breast patterns in Charadriinae. (A) *Charadrius hiaticula*; similar patterns = *C. collaris, C. dubius, C. placidus, C. semipalmatus, C. thoracicus, C. wilsonia.* (B) *C. vociferus*; similar patterns = *C. tricollaris.* (C) *C. melodus.* (D) *C. pecuarius*; similar pattern = *C. sanctaehelenae.* (E) *C. alexandrinus*; similar pattern = *C. marginatus, C. peronii.* (F) *C. venustus.* (G) *C. bicinctus.* (H) *C. falklandicus.* (I) *C. leschenaultii*; similar pattern = *C. mongolus.* (J) *C. asiaticus*; similar pattern = *C. veredus.* (K) *C. modestus.* (L) *C. montanus.* (M) *C. melanops.* (N) *C. cinctus.* (O) *C. rubricollis.* (P) *C. novaeseelandiae.* (Q) *Anarhynchus frontalis.* (R) *Phegornis mitchelli.* (S) *Pluvialis dominica*; similar pattern = *P. apricaria.* (T) *P. squatarola.* (U) *P. obscura.* (V) *Eudromias morinellus.* (W) *Oreopholus ruficollis.* (X) *Pluvianellus socialis.*

eye outline interrupted by a black line and six additional species have the dark eye against a uniform dark background (Table 1). Either of these two strategies would tend to conceal the eye. The fact that several of these species have colored eye rings does not detract from this function, since the colors cannot be seen at a distance.

In at least 24 of the species the head and breast colors are either absent or subdued in the non-breeding season as compared to the breeding plumage (Appendix I). In addition, immatures in at least 35 species differ from their respective adult breeding plumages (Appendix I). These data support the hypothesis that the patterns are mainly functional for adults during the nesting season.

Table 1

Summary of Breeding Adult Head and Breast Markings in Charadriinae

	Charadrius	Other Charadriinae	Totals
Number Species in Group	28	9	37
Lore-line Present	19	2	21
Black Crown Patch Present	21	0	21
Uniform Dark Face	3	3	6
Breast Band Present	18	3	21
Eye Outline Interrupted by Black Line	24	3	27
Interrupted Head Pattern	27	9	36

Support for the theory that these patterns function as disruptive coloration during nesting comes from the correlation between the presence of breast bands and characteristics of the nest site. Table 2 shows that those species that nest on a discontinuous substrate (Appendix II) tend to have breast bands while those that nest on uniform substrates (Appendix II) tend to lack breast bands. Discontinuous substrates are defined as having many contrasts between light and dark colors (shingle, disturbed areas, stony areas) whereas uniform substrates have no great contrast between light and dark colors (sand expanses, uniform grasslands, holes). A Chi-square Test of Independence shows that the difference is significant ($P < 0.025$). Two species were omitted from Table 2 because of a lack of good nest-site information and six species were omitted because they cannot be placed into one of the two substrate classifications, since they commonly nest near conspicuous dark objects (pebbles, sea drift, shrubs) on an otherwise uniform substrate such as fine sand (Appendix II). This correlation tends to support Huxley's (1958) suggestion that the breast bands in the Killdeer (*C. vociferus*) have a disruptive function.

Indirect evidence supports the hypothesis that some of the head and breast

Table 2

Presence of Breast Bands vs. Nest Site Location*

	Discontinuous Nest Substrate	Uniform Nest Substrate	Subtotals
Breast Band Present	13	4	17
Breast Band Absent	4	8	12
Subtotals	17	12	29

* Compiled from data in Appendix II.

Fig. 2. Horizontal threat display given by the Mountain Plover.

markings in this group also have social signal functions. For instance, in those cases where both sexes incubate (the normal situation in this group) identical head and breast markings would be expected if their sole function is disruptive coloration. In at least 27 cases where both sexes are reported to incubate, however, the male has brighter head and/or breast markings than the female (Appendix I). In the Dotterel (*Eudromias morinellus*) the male usually incubates alone (Pulliainen, 1970) and the female has brighter markings. Since sexual differences do exist it is likely that the differences enhance sexual recognition.

In at least the Killdeer and the Banded Dotterel (*Charadrius bicinctus*) the breast bands appear to reinforce aggressive displays, since in both species the bands are enlarged in threat postures (R. E. Phillips, pers. comm.).

In the Mountain Plover the facial markings seem to serve as reinforcers for threat displays. Males are more aggressive than females and males have brighter facial and breast markings. The most common threat display in this species (the Horizontal Threat—Fig. 2) presents a bold black and white image to the threatened bird. Another aggressive posture in this species (the Upright Threat), whereby two opponents stand close together and face each other with the bodies nearly vertical, also presents the bold facial markings to both participants. Both of these displays, or similar versions, have been described for the following additional species: the Kentish Plover (*C. alexandrinus*) (Rittinghaus, 1961), the Little Ringed Plover (*C. dubius*) (Simmons, 1953*a*), the Ringed Plover (*C. hiaticula*) (Simmons, 1953*b*), the Killdeer (Bunni, 1959), and the European Golden Plover (*Pluvialis apricaria*) (Bannerman, 1961). At least the Horizontal Threat, or a similar version, occurs in the Double-banded Plover (*C. bicinctus*) (R. E. Phillips, pers. comm.), the Black-fronted Dotterel (*C. melanops*) (R. E. Phillips, pers. comm.), the American Golden Plover (*P. dominica*) (Drury, 1961), the New

Zealand Dotterel (*P. obscura*) (R. E. Phillips, pers. comm.), and the Black-bellied Plover (*P. squatarola*) (Drury, op cit.). I suspect that future research will demonstrate that most of the Charadriinae species have aggressive displays in which a frontal view is presented to the opponent. It is perhaps significant that the black crown patch in 21 of the species of *Charadrius* is restricted to the front edge of the crown—the maximum black and white contrast is apparent only in a frontal view.

In the Mountain Plover the social signal function of the facial markings may be more important than the disruptive coloration function. The black lore line and black crown patch are conspicuous during the courtship period, but a molt of the head feathers begins soon after incubation starts and many individuals lack the bold markings before the end of incubation.

Bock (op. cit.) proposes that the Little Ringed Plover, the Ussuri Sand Plover (*C. placidus*), the Wilson's Plover (*C. wilsonia*) and the Killdeer currently represent the basic *Charadrius* stock from which the other species of *Charadrius* have radiated. Maclean's (1972) suggestion that species of Charadrii with reduced clutches have evolved from four egg species does not conflict with Bock's scheme.

Bock's proposal would suggest that the primitive *Charadrius* stock had breast bands, black lore lines and crown patches, since all living members of his basic stock have these features (Fig. 1). Thus, as species evolved in habitats with uniform, light colored substrates, selection would have favored the reduction or complete loss of the breast bands and dark facial marks. This would explain why the Piping Plover (*C. melodus*) has only a faint lore line and sometimes lacks a breast band and why the Kentish Plover, the White-fronted Plover (*C. marginatus*), and the Malay Sand Plover (*C. peronii*) have an incomplete breast band (Fig. 1)—all nest on light colored substrates.

Since the facial markings of many adults are bright only during the breeding season and in many species the immatures lack the markings, I doubt that the lore lines in these species of Charadriinae can serve as sight lines for capturing prey (Ficken and Wilmot, op. cit.; Ficken et al., op. cit.). It is hard to conceive that these species require sight lines for feeding only during the breeding season, especially since other functions appear to exist for the lore lines at this time.

SUMMARY

The 37 species in the subfamily Charadriinae are compared and possible functions of the head and breast patterns are reviewed. It appears that these patterns disrupt the body and eye outlines, which is especially important for the nesting bird. In some species the patterns may enhance sex recognition and may serve as reinforcers for aggressive displays. It is proposed that the primitive *Charadrius* stock had breast bands and nested

on shingle and that as this genus radiated the markings took on social signal functions and were modified by new selective pressures in new habitats. It appears doubtful that the black lore lines have any value as feeding sight lines among the Charadriinae species.

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Appendix I

Seasonal, Sexual, and Age Plumage Difference in Charadriinae

Species	Sexual Plumage Differences in Breeding Season	Breeding Plumage Brighter than Non-breeding	Immature Plumage Different than Adult Breeding Plumage	References*, **
Charadrius hiaticula	Yes	No	Yes	1, 5
C. semipalmatus	Yes	Yes	Yes	30, 31
C. placidus	Yes	Yes	Yes	5
C. dubius	Yes	Yes	Yes	1, 31
C. wilsonia	Yes	Yes	Yes	2, 30
C. vociferus	No	No	Yes	2, 30
C. melodus	Yes	Yes	Yes	2, 30
C. thoracicus	?	?	?	3, 27
C. pecuarius	No	No	Yes	4, 16, 17
C. sanctaehelenae	No	?	Yes	25
C. tricollaris	Yes	?	Yes	16, 29
C. alexandrinus	Yes	Yes	Yes	28, 30
C. marginatus	Yes	Yes	Yes	15, 29
C. peronii	Yes	Yes	Yes	12, 20, 29
C. venustus	Yes	?	Yes	16
C. collaris	Yes	Yes	Yes	9, 23
C. bicinctus	Yes	Yes	Yes	8, 23
C. falklandicus	Yes	Yes	Yes	9, 12, 13, 29
C. mongolus	Yes	Yes	Yes	5, 26
C. leschenaultii	Yes	Yes	Yes	5, 15
C. asiaticus	Yes	Yes	Yes	1, 5
C. veredus	Yes	Yes	Yes	5, 21
C. modestus	No	Yes	Yes	6, 13, 29

Appendix I—*Continued*

Species	Sexual Plumage Differences in Breeding Season	Breeding Plumage Brighter than Non-breeding	Immature Plumage Different than Adult Breeding Plumage	References*, **
C. montanus	Yes	Yes	Yes	10
C. melanops	Yes	Yes	Yes	11, 14, 19, 29
C. cinctus	No	No	Yes	18, 19, 29
C. rubricollis	No	No	Yes	14, 19, 29
C. novaseelandiae	Yes	No	Yes	8, 23, 24
Anarhynchus frontalis	Yes	Yes	Yes	22, 23
Phegornis mitchelli	Yes	?	Yes	6, 9, 13, 29
Pluvialis apricaria	Yes	Yes	Yes	1, 31
Pluvialis dominica	Yes	Yes	Yes	2, 7, 30
Pluvialis squatarola	Yes	Yes	Yes	2, 30
Pluvialis obscura	Yes	Yes	Yes	23, 29
Eudromias morinellus	Yes	Yes	Yes	1, 31
Oreopholus ruficollis	No	?	?	6, 9, 13, 17
Pluvianellus socialis	No	?	Yes	6, 9, 12, 13

* Gooders, J. 1969. Birds of the world, Vol. 3 (Parts 6 and 7), IPC Magazines Ltd., London. Contains photographs and drawings of most Charadriinae species and is used here as a general reference.

** References listed in Appendix I as follows:

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2. Bent (1929)
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31. Witherby et al. (1941)

Appendix II

Breast Band Presence, Main Nest Site, and Nest Site References

Species	Breast Band (× = Present)	Main Nest Site*	Nest Site References**
Charadrius hiaticula	×	Shingle (1)	1, 33
C. semipalmatus	×	Shingle (1)	8, 29
C. placidus	×	Shingle (1)	6
C. dubius	×	Shingle (1)	1, 28, 33
C. wilsonia	×	Sand (frequently near dark objects) (3)	2, 30
C. vociferus	×	Shingle or disturbed areas (1)	4, 8
C. melodus	Usually	Sand (2)	2, 31
C. thoracicus	×	Sub-desert (?)	24
C. pecuarius		Sand (2)	9, 32
C. sanctaehelenae		Grasslands (2)	21
C. tricollaris	×	Shingle, dried mud (1)	3
C. alexandrinus	incom.	Sand, salt flats (2)	12, 25
C. marginatus	incom.	Sand (near objects) or shingle (3)	14, 27
C. peronii	incom.	Sand (near drift) (3)	17
C. venustus	×	Salt pans (2)	3, 13
C. collaris	×	Sand, river beds (?)	7
C. bicinctus	×	Shingle, disturbed areas, sand (1)	19
C. falklandicus	×	Sand, short grass (2)	5, 15
C. mongolus		Stony tundra (1)	6, 22
C. leschenaultii		Stony areas (1)	6
C. asiaticus	×	Arid grasslands (commonly among pieces of clay) (1)	6, 33
C. veredus	×	Stony areas (1)	6
C. modestus	×	Arid grasslands (2)	5
C. montanus		Arid grasslands (2)	8
C. melanops	×	Shingle, dried mud, sand (1)	12, 19
C. cinctus	×	Sand (commonly near shrubs) (3)	16
C. rubricollis	incom.	Sand (near sea drift commonly) (3)	26

Appendix II—*Continued*

Species	Breast Band (× = Present)	Main Nest Site*	Nest Site References**
C. novaseelandiae		Holes or crevices (2)	19
Anarhynchus frontalis	×	Shingle (1)	18, 19
Phegornis mitchelli	×	Shingle or rocky sand areas (1)	10, 11
Pluvialis apricaria		Moors (2)	1, 33
Pluvialis dominica		Stony tundra (1)	8, 20
Pluvialis squatarola		Stony tundra (1)	8, 20
Pluvialis obscura		Sand (2)	19
Eudromias morinellus	×	Arid areas (commonly stony) (1)	1, 23
Oreopholus ruficollis		Arid grassland (2)	11
Pluvianellus socialis		Sand (sometimes near rocks) (3)	11

* (1) = Nest site considered discontinuous.
(2) = Uniform nest site substrates.
(3) = Nest sites near conspicuous dark objects on an otherwise uniform substrate.

** References in Appendix II:

1. Bannerman (1961)
2. Bent (1929)
3. Blaker (1966)
4. Bunni (1959)
5. Cawkell and Hamilton (1961)
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28. Simmons (1953*a*)
29. Sutton and Parmelee (1955)
30. Tompkins (1944)
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